



RESEARCH ARTICLE

## Radio-tracking reveals insight into survival and dynamic habitat selection of fledgling Cerulean Warblers

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### ABSTRACT

For most bird species, little is known about their ecology and survival between fledging and independence despite the potential for post-fledging survival to be a factor limiting population dynamics. Cerulean Warblers (*Setophaga cerulea*) are a declining migratory species, and full-life-cycle conservation efforts that include the post-fledging period are warranted to attempt to reverse their decline. To understand movement, habitat selection, and survival, we radio-tracked 20 fledglings throughout the dependent post-fledging period. Broods were split by their parents, typically (88%) left parental breeding territories within 12 days, and survivors moved  $2.4 \pm 0.7$  km (mean  $\pm$  SE) from their nest within the  $28.1 \pm 1.8$  day tracking period. Fledglings were usually observed in the mid-canopy to upper canopy and selected habitat with greater mid-story cover, less basal area, and areas closer to water bodies, compared to available points, when considering data from the entire post-fledgling period. However, habitat selection varied with fledgling age. Young fledglings (0–2 days post-fledging) selected areas with greater sapling cover and less stand basal area, but as fledglings matured, they selected areas farther from canopy gaps with greater mid-story cover. Compared with nesting habitat selected by parents, fledglings used areas with smaller and more numerous trees, fewer canopy gaps, and greater mid-story cover. Survival of the entire period was  $48 \pm 14\%$  and most (8/10) mortalities occurred within the first 3 days post-fledging. Evidence indicated eastern chipmunks (*Tamias striatus*) as the most common predator. Providing or retaining large tracts of forest is recommended to prevent the restriction of post-fledging dispersal, and managing forests to maintain a heterogeneous landscape that includes stands with numerous canopy gaps and dense understory (e.g., shelterwood harvests or late seral stage conditions) as well as stands with a dense mid-story (e.g., younger stands and riparian areas) appears to be important for this life stage.

**Keywords:** Cerulean Warbler, dispersal, habitat selection, post-fledging, survival

### El seguimiento por radio revela pistas de la supervivencia y la dinámica de selección de hábitat de volantones de *Setophaga cerulea*

### RESUMEN

Para la mayoría de las especies de aves, poco se sabe de la ecología y supervivencia entre el emplumamiento y la independencia, a pesar de que la supervivencia post-emplumamiento puede ser un factor que limita potencialmente las dinámicas poblacionales. *Setophaga cerulea* es una especie migratoria en disminución, y los esfuerzos de conservación del ciclo de vida completo que incluyen el periodo post-emplumamiento son importantes para intentar revertir su declive. Para entender el movimiento, la selección de hábitat y la supervivencia, seguimos por radio 20 volantones a través del periodo de dependencia post-emplumamiento. Las nidadas fueron divididas por sus progenitores, típicamente (88%) dejaron los territorios de cría de sus progenitores dentro de los 12 d, y los sobrevivientes se movieron  $2.4 \pm 0.7$  km (media  $\pm$  EE) desde sus nidos dentro de los  $28.1 \pm 1.8$  d del periodo de seguimiento. Los volantones fueron usualmente observados en el dosel medio y alto y seleccionaron hábitats con mayor cobertura del estrato medio, con menor área basal y más cercanas a cuerpos de agua, en comparación con los puntos disponibles, al considerar los datos para todo el periodo post-emplumamiento. Sin embargo, la selección de hábitat varió con la edad del volantón. Los volantones jóvenes (0–2 d post-emplumamiento) seleccionaron áreas con mayor cobertura de renovales de árboles y menor área basal del rodal, pero a medida que los volantones maduraron, seleccionaron áreas más lejanas de las aperturas del dosel y con mayor cobertura del estrato medio. En comparación con el hábitat de anidación seleccionado por los progenitores, los volantones usaron áreas con árboles más chicos y más numerosos, con menor apertura del dosel y con mayor cobertura del estrato medio. La supervivencia de todo el periodo fue de  $48 \pm 14\%$  y la mayoría de la

mortalidad (8/10) ocurrió dentro de los primeros tres días post-emplumamiento. La evidencia indicó a la ardilla *Tamias striatus* como el depredador más común. Se recomienda proporcionar o retener grandes extensiones de bosque para prevenir la restricción de la dispersión post-emplumamiento. Además, parece ser importante para este estadio de vida manejar los bosques para mantener un paisaje heterogéneo que incluya rodales con numerosas aperturas en el dosel y sotobosque denso (e.g., cosecha de árboles del dosel o condiciones de etapas sucesionales tardías) así como rodales con un estrato medio denso (e.g., rodales más jóvenes y áreas ribereñas).

**Palabras clave:** dispersión, post-emplumamiento, selección de hábitat, *Setophaga cerulea*, supervivencia

## INTRODUCTION

Over the course of their complex life cycles and annual cycles that include nesting, post-fledging, molt, migration, and overwintering periods, the habitat features required and preferred by migratory birds often change as individuals transition between life history periods (Pagen et al. 2000, Vitz and Rodewald 2007, Marra et al. 2015). Understanding this dynamism takes on applied importance when attempting to develop habitat management recommendations that consider all life-history periods of species of conservation concern. For many declining songbird species, we know little about the post-fledging period, which may be just as important to the conservation of avian species as the better-studied nesting period (Yackel Adams et al. 2006, McKim-Louder et al. 2013).

Young birds of species typically considered denizens of the forest interior (e.g., Wood Thrush [*Hylocichla mustelina*] and Ovenbird [*Seiurus aurocapilla*]) often move from their natal habitat, which consists of nearly complete overstory cover and little understory cover, to areas with decreased overstory canopy cover and dense mid-story or understory cover (Vega Rivera et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2011). In addition, although we often consider the post-fledging period as a single, unified stage, this period is likely more dynamic. As young birds develop, their mobility, naiveté, and selective pressures may change rapidly. For example, juvenile birds are not very mobile over the first week post-fledging, when they are most susceptible to predation (Moore et al. 2010, Ausprey and Rodewald 2011, Eng et al. 2011) and are not able to move far from their respective nests. However, as mobility of fledglings increases they become better able to exploit other, potentially more distant, habitats that could reflect a balance between protection from predators (Martin 1988, Anders et al. 1998, King et al. 2006) and food availability (Vega Rivera et al. 1998). As their risk of predation further decreases with age, fledglings may shift the focus of their selection strategies from predator avoidance toward greater food availability (Streby et al. 2011) as they learn to forage for themselves and transition toward independence as they physiologically prepare for their first migration. Thus, it can be hypothesized that habitat selection may vary even *within* the dependent post-fledging period (King et al. 2006, Ausprey and Rodewald 2011).

Ultimately, the selection of habitat and specific habitat features during the early (i.e. dependent) post-fledging period should reflect the relative importance of different selective pressures that influence an individual's chance of survival. For example, for understory species, mortality rates during the early post-fledging period can be especially high, largely because of predation, and most instances of predator-related fledgling mortality occur within the first 3 weeks after leaving the nest (Cox et al. 2014). However, there is currently little information about habitat selection or survival of canopy-dwelling fledglings. Capturing nestlings or fledglings of species belonging to this guild is challenging and following fledglings in an unbiased manner may only be possible through tracking via radio telemetry because they are otherwise difficult to reliably detect (White and Faaborg 2008) or recapture (e.g., traditional passive mist-netting). Prior to miniaturization of very high frequency (VHF) radio-tracking devices, attempts at modeling songbird population dynamics often resorted to assuming juvenile survival to be 25–50% of observed estimates of adult survival (Ricklefs 1973, Greenberg 1980, Temple and Cary 1988, Buehler et al. 2008). However, with recent increases in post-fledging tracking studies, it is now clear that post-fledging survival is highly variable across species, regions, and years (23–87% survival during the first 3 weeks post-fledging; Cox et al. 2014). This makes estimation of species- or population-specific post-fledging survival rates a critical step in the eventual production of more accurate full-life-cycle population models (e.g., Taylor and Stutchbury 2016).

The canopy-dwelling Cerulean Warbler (*Setophaga cerulea*) is one of the fastest-declining long-distance migratory birds in North America (–2.6% per year from 1966 to 2015; Sauer et al. 2017) and is considered a species of conservation concern and vulnerable to extinction by numerous organizations (Buehler et al. 2013, Rosenberg et al. 2014, BirdLife International 2016). Habitat loss and degradation in both breeding and nonbreeding regions used by this species are thought to be the primary causes of the species' decline (Hamel 2000). Most recent research on the species has focused on identifying factors that limit the species' population(s) and developing species-specific forest management guidelines to increase breeding territory densities and improve nesting success (e.g., Hartman et al. 2009, Boves and Buehler 2012, Boves et al. 2013a,

Wood et al. 2013). However, important gaps in our knowledge during the reproductive season still exist, particularly with respect to the post-fledging period.

In this study, we used radio telemetry to track fledgling Cerulean Warblers to (1) quantify movement patterns (e.g., distance), (2) assess age-dependent habitat selection and compare habitat at nest locations with habitat at locations used by fledglings, and (3) estimate a minimum survival rate for Cerulean Warblers during the dependent post-fledging period. We also report nest survival estimates. Our findings are valuable for guiding ongoing conservation efforts that target this declining species by providing (1) information to support refinements to existing forest management guidelines that account for habitat selection and survival during the post-fledging period; and (2) an estimate of post-fledging survival and nest success as inputs for future full reproductive season productivity estimates, and, ultimately, full-life-cycle population models (e.g., Hostetler et al. 2015, Rushing et al. 2016).

## METHODS

### Focal Species

Across their breeding grounds in eastern North America, Cerulean Warblers establish territories and build nests in the upper canopy of deciduous forests. Adult Cerulean Warblers prefer ridgetops or river valleys, and north- to east-facing slopes amid contiguous forest, and, at the territory scale, a heterogeneous canopy structure (Boves et al. 2013a, Buehler et al. 2013). Cerulean Warblers often engage in extra-pair copulations, but generally only one male assists the female with nestling and fledgling provisioning and is referred to as the social father.

Females typically select nest sites in the canopy of large trees ( $44.0 \pm 0.7$  cm DBH [diameter at breast height]) located in patches characterized by decreased basal area ( $20.7 \pm 0.4$  m<sup>2</sup> ha<sup>-1</sup>), decreased mid-story cover ( $45 \pm 1\%$ ), and increased understory cover ( $47 \pm 1\%$ ) at nest sites (Boves et al. 2013a).

### Study Area

Our study area comprised 3 sites on the Allegheny Plateau in northwestern Pennsylvania, USA. The sites were all located within a heavily forested landscape (>85% forest cover within 5 km) and consisted of a mosaic of mature oak-dominated hardwood forest interspersed with patches of younger regenerating forest of varying size and age (resulting from timber harvest, prescribed burns, or both). We focused our efforts in areas previously known to harbor relatively high densities of Cerulean Warblers (S. H. Stoleson personal observation) in order to maximize the number of nests we could potentially locate. All study sites were within local landscapes (within 40 km) that contained a mixture of

managed (i.e. timber harvests in various stages of regeneration and/or prescribed fire) and undisturbed mature forest stands. By selecting study sites that met these criteria, all fledglings we monitored had multiple habitat options. The first site, State Game Lands No. 86 (SGL 86; 41.8°N, 79.3°W) was 14,271 ha in size, included a steep east-facing slope rising from the Allegheny River, and extended onto the top of the plateau, with numerous stream valleys cutting through its edge. We focused our nest-searching efforts on ~220 ha of SGL 86 that included 3 mature, oak-dominated forest stands of ~35–45 ha that were managed using shelterwood and group selection harvests of different ages (2–12 yr since harvest). Two of these stands contained relatively high densities of Cerulean Warblers (0.25–0.37 territories ha<sup>-1</sup>), and the third had a few territories within the stand and ~10 territories within 500 m of its edge. Territory density estimates are based on intensive nest-searching, color-banding, and resighting efforts for both this and a concurrent study (Raybuck et al. 2017).

Our second site was located on the Allegheny Plateau within the Allegheny National Forest. Within an expansive forested area, we focused our nest-searching efforts on ~220 ha along Forest Road 449 (41.6°N, 79.2°W). This area included a variety of stands that had been recently managed using prescribed burns (one of which was partially harvested prior to burning), deer exclusion fences to promote understory regeneration, shelterwood harvests, and forest road corridors (i.e. linear anthropogenic canopy gaps). Cerulean Warbler territory densities at this site were relatively low, with an estimated 0.09 territories ha<sup>-1</sup>.

The third site (Longhouse; 41.8°N, 79.0°W) was also in the Allegheny National Forest and located along the Kinzua Reservoir, a 5,000-ha lake formed by the damming of the Allegheny River. It was characterized by a steep east-facing slope with mature, oak-dominated forest that had not been disturbed in the recent past, but there was a recently burned managed stand within 800 m of the center of our nest-searching area. Here, we focused our nest-searching efforts in an area of ~60 ha with relatively high densities of Cerulean Warbler territories (~0.25 territories ha<sup>-1</sup>), which was intersected by 2 paved roads and a ~15-m-wide powerline (and associated roadside and right-of-way vegetation disturbances).

### Field Methods

We conducted field work from May 8 through August 8 during the 2014 and 2015 breeding seasons. We searched for nests at each study site by following aural and visual cues of adults throughout the nesting season and found most nests by following females during the nest-building period or by following either parent during the nestling provisioning period. With equal effort, we attempted to



locate nests associated with each singing male within our sites (44 of 73 nests were associated with males uniquely color-banded for a concurrent study; Raybuck et al. 2017). We were successful in finding nests in most territories (~75%).

Once a nest was located, we monitored it every 1–3 days to estimate hatch dates (based on number of days incubating; King et al. 2006, Streby and Anderson 2013) and to predict fledge dates (based on number of days with nestlings). As predicted fledge date approached, nests were monitored daily with observers ready to opportunistically capture and radio-tag fledglings upon leaving their nests. Some fledglings came down from the nest to the ground or within our reach in the under- or mid-story and were hand-captured. For those that did not descend to within reach, when possible, we used a ~15-m-long telescoping pole with telescoping net attached to capture fledglings. Although ideal, randomly selecting a single fledgling from each nest for capture was not possible because over 50% of fledglings remained out of our reach, flying tree-to-tree at nest height (often >18 m above ground). Because we could not capture the fledglings that did not descend from the upper canopy, we consider our survival estimates to be minimal because predators may also be less likely to capture fledglings that eluded us and were potentially in better condition (Naef-Daenzer et al. 2001).

Upon capture, we attached 0.35-g or 0.39-g VHF transmitters (4–5% of body mass, ~30-day battery life; Blackburn Transmitters, Nacogdoches, Texas, USA) to fledglings using 1-mm-diameter elastic cord in a modified Rappole and Tipton (1991) leg-loop harness that has only minimal effect on mobility (Rappole and Tipton 1991, Neudorf and Pitcher 1997). After tagging, we returned fledglings to locations as close to where they were captured as was feasible, which sometimes required using a portable ladder to reach the mid-story. We used portable TR-4 receivers outfitted with a directional RA-23K antenna (Telonics, Mesa, Arizona, USA) to track fledglings. Each day after capture, fledgling locations were recorded at the point where birds were first observed; we then marked these locations for vegetation/habitat variable measurements that we conducted on a later date. We recorded daily locations until one of the following occurred: (1) fledgling mortality, (2) transmitter loss, (3) battery failure, or (4) failure of detection potentially caused by dispersal from the search area. In the event of mortality, we attempted to recover the body and transmitter to infer cause (e.g., predator species). We did not measure habitat characteristics on days we found dead fledglings, as they may have been moved by predators or scavengers.

To determine selection of habitat features, we measured and compared vegetative and other habitat characteristics at observed fledgling locations with paired available points.

Based upon observed fledgling behavior and movement patterns (post hoc), we considered 5 fledgling age classes to determine the radius ( $r$ ) from the nest from which we selected our paired available points: 0–2 days, 3–6 days, 7–12 days, 13–20 days, and 21–36 days post-fledgling. For each fledgling, we considered available habitat to be a circular area, centered on the nest, with  $r$  = the maximum distance from the nest for which each individual fledgling had been observed within each respective age class. For each used location, we chose a paired available point described by 2 random numbers (generated at <https://www.random.org/>) that corresponded to the distance (in meters along both the  $x$ - and  $y$ -axes, between zero and  $r$ , and randomly either in a plus (+) or minus (–) direction) from the nest. If the randomly chosen location fell outside of the age-defined circle of “available” habitat (each initially chosen random point had the potential to fall within a square for which each side =  $2*r$  but outside the circle of radius  $r$ ), the location was rejected and the process was repeated until a location within the circle was chosen (see figure 13.6 in Pharr et al. 2016).

We measured habitat characteristics at each used and available point (and at nest sites) following similar methods to those employed in previous studies of breeding site selection by Cerulean Warblers that focused on characterizing 3-dimensional forest structure (e.g., Boves et al. 2013a). We included measurements of (1) stand basal area (BA) in  $\text{m}^2 \text{ha}^{-1}$  using a  $10\times$  or  $20\times$  cruising prism; (2) average and (3) maximum DBH (cm) of all trees ( $\geq 10$  cm DBH) within the prism plot; percent foliage cover in the (4) overstory (18+ m), (5) mid-story (6–15 m), and (6) under-story (2–5 m) layers; (7) percent shrub-layer cover (0.5–1.5 m) and (8) percent sapling cover ( $\geq 1.4$  m high and DBH < 10.0 cm) within 3 m of plot center; (9) Beers’ slope aspect (measured with a compass and transformed; Beers et al. 1966); (10) distance (m) to nearest canopy gap; (11) average canopy height within the prism plot (m, measured with clinometer); (12) distance (km) to nearest stream (third-order or greater; Strahler 1957; measured in Google Earth Pro [<https://www.google.com/earth/>]); and (13) topographic slope (degrees, measured with a clinometer). For foliage cover measurements at each of the 3 strata, we used a sighting tube at 21 locations within 0.04 ha (one measurement at plot center and 5 measurements spaced equally for 11.3 m in each cardinal direction) to detect presence/absence of overhanging foliage. All vegetation measurements were conducted within 4 weeks of the associated fledgling location observation or nest fate date (June 28 to August 5). During the first week after fledgling (when birds were still quite immobile), we did not measure habitat until fledglings had dispersed from the area to reduce the likelihood of our presence influencing a fledgling’s movements and survival.

## Data Analysis

**Fledgling movements.** To describe spatial movements of fledglings across the landscape, we measured distance between locations in Google Earth Pro. For one randomly selected fledgling per brood (among fledglings surviving >1 day), we measured maximum observed distance from the nest at each age class and distance moved between daily locations and calculated means for each age class. In cases of a 1-day gap in daily locations ( $n = 4$ ), we divided the distance between locations on the day prior to, and after, the missing location by 2 for estimation of the distance between the missing location and the next recorded location. We did not estimate distance between locations for instances ( $n = 4$ ) of multi-day gaps in observed locations.

**Post-fledgling habitat selection.** To evaluate habitat selection over the post-fledging period, we compared habitat variables at used and paired available points using generalized linear mixed models (GLMM), with point status (used vs. available) as a binary response variable and bird ID and brood ID included as random effects, in the package *lme4* in Program R 3.2.3 (Bates et al. 2015, R Core Team 2016). We considered linear relationships for all 13 variables, and a quadratic relationship for stand basal area because adult Cerulean Warblers have been found to select territories in stands with an intermediate level of stand basal area (Boves et al. 2013b). We constructed and compared suites of models describing habitat selection behavior over the entire (1) monitoring period and (2) for each fledgling age class and compared models and parameter estimates (magnitude and directionality of  $\beta$ ) to ascertain if habitat selection behavior differed among age classes. In each case, we first compared all univariate (13) and bivariate (78) models (and an intercept-only null model) and ranked them using Akaike's information criterion (adjusted for small sample size;  $AIC_c$ ). We considered all models with  $\Delta AIC_c$  values  $\leq 2$  to be equivalent (Burnham and Anderson 2002). We also constructed and compared more complicated models (i.e. >2 covariates), with all possible combinations of variables included in the top equivalent univariate or bivariate models as well as any variables whose 85% confidence interval (CI) of the  $\beta$  did not overlap zero in their univariate model. We chose 85% CI because it is more compatible with AIC-based model selection than 95% CI (Arnold 2010). From all of the final top equivalent models, we examined 85% CI of all  $\beta$  values to compare relative importance and directionality of selection of each variable; those variables for which the 85% CI of the  $\beta$  overlapped zero we considered to be uninformative (Arnold 2010). We do not report more complicated (less parsimonious) models that only differed from a more parsimonious model by one variable with an 85% CI that overlapped zero. For all variables that were included in more than one top equivalent model, we only report the  $\beta$  (and 85% CI) for the model with the lowest  $AIC_c$  value.

**Post-fledgling vs. nesting habitat.** Additionally, to determine whether fledglings (or family groups with fledglings) selected habitat that differed from those adults used for nesting (used vs. nest), we constructed all univariate models in a similar fashion as the habitat selection analysis (used vs. available), but with only brood ID as a random effect. We then examined the  $\beta$  (and 85% CI) from each model and considered the habitat measurements used by fledglings to be different from nesting habitat when the 85% CI did not overlap zero. We compared habitat characteristics between nest and fledgling locations over the entire tracking period as well as for each individual age class and reported habitat variable means  $\pm$  SE for each age class for direct comparison.

**Fledgling survival.** We estimated minimum survival rate(s) over the first 17 days of the post-fledging period by comparing known-fate constant, age class-specific, and daily variation survival models in program MARK (White and Burnham 1999). For age class-specific models, we included models with constant survival (a single 0–17 day period), 2 age classes (0–2 and 3–17 days), 3 age classes (0–2, 3–6, and 7–17 days), and 4 age classes (0–2, 3–6, 7–12, and 13–17 days). We calculated 85% CI from a beta distribution created with 10,000 Markov chain Monte Carlo simulations of mean and SE (Amundson and Arnold 2011) and considered age class-specific survival to differ if the 85% CI for each age class did not overlap. We used model averaging to derive survival estimate from the top equivalent models ( $\leq 2.00 AIC_c$ ). We did not include data from individuals  $\geq 18$  days post-fledging because detectability was <100% due to fledgling movements of up to several kilometers per day during this age class, variable pulse detection distances caused by rugged terrain (~200–1,000 m), and variation in transmitter battery life and signal strength. This initial 17-day period includes a majority of the dependent post-fledging period (independence from parents was reached at ~25–28 days) and spans the period of highest mortality (Cox et al. 2014). However, the entire period between fledging and initiation of migration likely spanned at least 60 days: from mid-June through early July fledging events until mid-August to early September initiation of migration, based on our unpublished geolocator-derived data obtained from adult males.

With the intention of avoiding potential bias in survival estimate variation due to possible non-independent fates of brood-mates, we randomly selected one fledgling per brood to include in our survival analysis. This reduced our sample size to 14 fledglings so, for comparison, we also ran the analyses with the inclusion of brood-mates, assuming independent fates (e.g., supported by survival data for Hooded Warblers [*Setophaga citrina*]; Eng et al. 2011) to increase sample size to 20 fledglings and, potentially, the accuracy and precision of

survival estimates. For the analysis that included brood-mates, if fates were not independent (5 of 6 brood-mate pairs had similar fates), the survival estimate should not change, but we may have underestimated the associated variation around the mean (Flint et al. 1995, Anders et al. 1997, Johnson 2002).

Finally, we evaluated relationships between habitat variables and survival during the first 3 days after fledging (period of highest mortality in our study). To characterize habitat features associated with fledgling survival, we compared models that included all combinations of habitat covariates that we deemed to be important in the previous habitat selection analysis (i.e. sapling cover, mid-story cover, canopy height, and BA) associated with days each fledgling was still alive during ages 0–2 days. Although we did not include habitat characteristics on days we found the dead fledglings because the bodies may have been moved post-mortem, habitat conditions were likely similar in the previous days because the fledglings did not move far over this time period ( $45 \pm 11$  m from the nest).

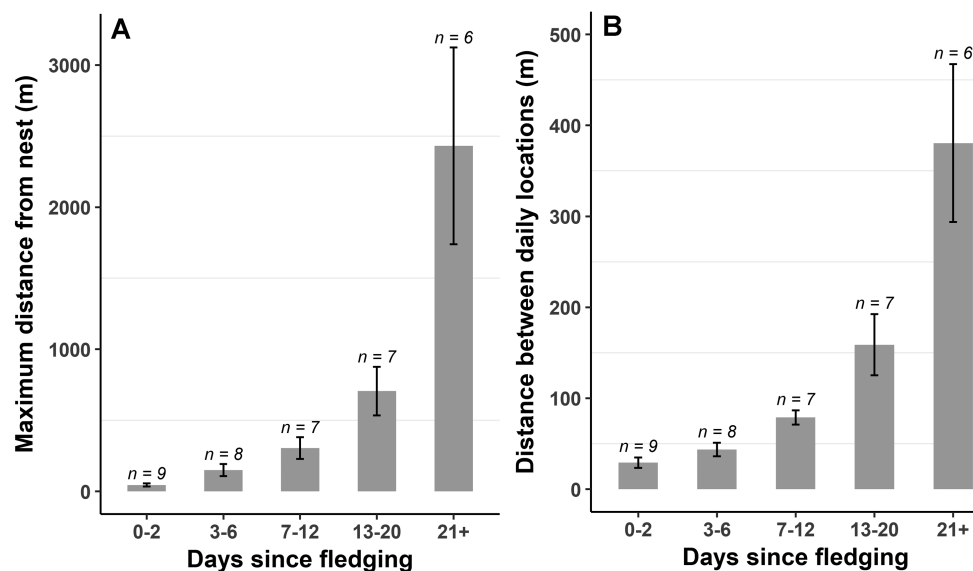
**Nest productivity.** We estimated nest success and mean number of fledglings produced per successful nest to provide regional inputs for use in future full breeding season productivity and full-life-cycle modeling efforts. To estimate daily nest survival, we constructed and compared 2 logistic exposure models (one with and one without a year effect) in the nest survival module in Program MARK (Dinsmore and Dinsmore 2007) and considered yearly estimates to be the same if the 85% CI overlapped zero. We estimated cumulative nest success

by raising the daily nest survival estimate to the 25th power based on the average number of combined egg and nestling exposure days from this study and approximated the cumulative nest success standard error using the delta method (Powell 2007). We determined number of fledglings produced per successful nest by counting juveniles on the date of fledging events. All means are reported  $\pm$  SE.

## RESULTS

### Fledgling Movement

We captured and tracked 20 fledglings from 14 different broods over 2 field seasons. Fledglings followed exponential patterns of both maximum distance from the nest and distance between daily locations as they aged (Figure 1). During ages 0–2 days post-fledging, juveniles remained within  $45 \pm 11$  m from the nest; during ages 3–6 days, brood division occurred for most family groups, with some ( $n = 6$ ) radio-tracked fledglings following the mother and some ( $n = 6$ ) following the social father up to  $150 \pm 42$  m from the nest. By ages 7–12 days, most fledglings (88%) had dispersed beyond their social father's breeding territory (up to  $305 \pm 76$  m from the nest). During ages 13–20 days, fledglings were often located in areas where we never detected singing males during the nesting period ( $717 \pm 169$  m from the nest). By the end of the tracking period ( $28.1 \pm 1.8$  days, maximum = 36 days), the average maximum distance fledglings had moved from their nest was  $2.4 \pm 0.7$  km (range: 1.0–5.3 km).



**FIGURE 1.** Mean fledgling movements, with standard error bars, of 9 fledgling Cerulean Warblers (from unique broods) that survived >2 days post-fledging in northwestern Pennsylvania, USA. Both (A) maximum distance recorded from the nest and (B) distance between daily locations increased with each age class.

### Post-fledging Habitat Selection

We measured habitat variables at 288 fledgling locations and an equal number of paired available points. Pearson's correlation coefficients between explanatory variables were  $<0.6$ . For all age classes combined, the sole top model explaining habitat selection included 3 important variables: basal area ( $24.4 \pm 0.7 \text{ m}^2 \text{ ha}^{-1}$  used,  $26.2 \pm 0.7 \text{ m}^2 \text{ ha}^{-1}$  available), mid-story cover ( $68.1 \pm 1.6\%$  used,  $63.3 \pm 1.7\%$  available), and distance to water ( $1.6 \pm 0.1 \text{ km}$  used,  $1.9 \pm 0.1 \text{ km}$  available; see [Tables 1](#) and [2](#)). At 0–2 days post-fledging, the sole top model included 2 important variables: canopy height ( $27.7 \pm 1.0$  used,  $29.2 \pm 0.9$  available) and sapling cover (used  $40.6 \pm 4.0\%$ , available  $27.3 \pm 3.6\%$ ). At ages 3–6 days, 7 models were equivalent and included 5 important variables, including BA ( $23.7 \pm 1.4 \text{ m}^2 \text{ ha}^{-1}$  used,  $19.9 \pm 1.8 \text{ m}^2 \text{ ha}^{-1}$  available), but with a negative relationship with quadratic BA, suggesting a threshold to their preference for more/larger trees. Other important variables at this age class were distance from canopy gaps ( $10.4 \pm 1.0 \text{ m}$  used,  $7.7 \pm 1.2 \text{ m}$  available), sapling cover ( $25.7 \pm 4.3\%$  used,  $39.7 \pm 4.8\%$  available), and greater Beers' aspect (i.e. preference for north- to east-facing slopes). At

ages 7–12 days, the sole top model included 2 important variables: Beers' aspect (again fledglings preferred north- to east-facing slopes) and maximum DBH ( $70.0 \pm 1.2 \text{ cm}$  used,  $63.2 \pm 1.7 \text{ cm}$  available). From ages 13–20 days, 2 equivalent top models included 2 important variables: mid-story cover ( $73.0 \pm 2.7\%$  used,  $66.1 \pm 3.3\%$  available) and sapling cover ( $30.6 \pm 3.5\%$  used,  $41.0 \pm 4.0\%$  available). From age 21 days until the end of the tracking period, 4 top models were equivalent and included 5 important variables: Beers' aspect (selected for north- to east-facing slopes), overstory cover ( $78.5 \pm 3.7\%$  used,  $88.5 \pm 2.5\%$  available), BA ( $23.8 \pm 1.6 \text{ m}^2 \text{ ha}^{-1}$  used,  $30.8 \pm 1.2 \text{ m}^2 \text{ ha}^{-1}$  available, and a positive relationship with quadratic BA), sapling cover (used  $42.2 \pm 3.5\%$ , available  $32.3 \pm 3.3\%$ ) and proximity to water ( $1.1 \pm 0.2 \text{ km}$  used,  $2.0 \pm 0.2 \text{ km}$  available).

**Post-fledging vs. adult nest site selection.** Fledgling habitat conditions differed from areas that adults chose for nesting locations (see [Table 1](#) and [Figure 2](#)). Overall, post-fledging habitat was characterized by smaller average DBH and greater BA, greater understory and mid-story cover, and closer proximity to water compared with nest

**TABLE 1.** Comparison of means  $\pm$  SE of habitat variables at nest, used, and available fledgling locations across Cerulean Warbler post-fledging age classes (days since fledging) in Pennsylvania, USA. DBH = tree diameter at breast height, BA = basal area.

Age	Average DBH (cm)	Maximum DBH (cm)	BA ( $\text{m}^2 \text{ ha}^{-1}$ )	Canopy height (m)	% Sapling cover
Nest	$54.1 \pm 2.3$	$71.0 \pm 3.3$	$18.7 \pm 2.4$	$29.5 \pm 1.2$	$31.1 \pm 8.3$
0–2 days	$47.1 \pm 2.2^a$	$68.5 \pm 2.9$	$21.1 \pm 1.6^b$	$29.4 \pm 0.7^b$	$40.6 \pm 4.0^b$
Available	$49.0 \pm 1.5$	$69.1 \pm 1.8$	$25.3 \pm 1.7$	$30.8 \pm 0.6$	$27.3 \pm 3.4$
3–6 days	$43.8 \pm 1.5^a$	$65.6 \pm 2.0$	$23.7 \pm 1.4^{ab}$	$29.2 \pm 0.9$	$25.7 \pm 4.3^b$
Available	$44.2 \pm 2.2$	$62.3 \pm 2.7$	$19.9 \pm 1.8$	$27.7 \pm 1.0$	$39.7 \pm 4.8$
7–12 days	$46.0 \pm 1.2^a$	$70.0 \pm 1.2^b$	$25.3 \pm 1.6^a$	$29.3 \pm 0.5$	$26.0 \pm 3.4$
Available	$44.2 \pm 1.6$	$63.2 \pm 1.7$	$24.1 \pm 1.6$	$29.3 \pm 0.8$	$32.0 \pm 3.8$
13–20 days	$40.9 \pm 1.3^a$	$64.2 \pm 1.9^a$	$26.7 \pm 1.4^a$	$27.3 \pm 0.8^b$	$30.6 \pm 3.5^b$
Available	$44.1 \pm 1.5$	$67.4 \pm 1.9$	$27.7 \pm 1.5$	$28.8 \pm 0.6$	$41.0 \pm 4.0$
21–36 days	$36.6 \pm 1.5^a$	$58.2 \pm 2.8^a$	$23.8 \pm 1.6^b$	$27.2 \pm 0.9$	$42.2 \pm 3.5^b$
Available	$37.9 \pm 1.2$	$61.2 \pm 2.2$	$30.8 \pm 1.2$	$28.2 \pm 0.6$	$32.3 \pm 3.3$
0–36 days	$42.3 \pm 0.7^a$	$64.9 \pm 1.0$	$24.4 \pm 0.7^{ab}$	$28.3 \pm 0.4$	$33.2 \pm 1.7$
Available	$43.4 \pm 0.7$	$64.5 \pm 0.9$	$26.1 \pm 0.7$	$28.9 \pm 0.3$	$34.7 \pm 1.8$
Age	% Understory	% Mid-story	% Overstory	Dist. to gap (m)	Dist. to water (km)
Nest	$42.2 \pm 8.7$	$49.2 \pm 6.8$	$81.0 \pm 2.7$	$4.5 \pm 1.3$	$2.1 \pm 0.2$
0–2 days	$53.7 \pm 3.8$	$58.1 \pm 4.8$	$77.6 \pm 4.1$	$10.8 \pm 1.7^a$	$2.1 \pm 0.3$
Available	$47.9 \pm 4.3$	$54.1 \pm 5.0$	$85.8 \pm 2.1$	$10.5 \pm 1.4$	$2.1 \pm 0.3$
3–6 days	$47.2 \pm 3.7$	$61.3 \pm 4.3^a$	$82.1 \pm 3.4$	$10.4 \pm 1.0^{ab}$	$1.6 \pm 0.2^a$
Available	$53.1 \pm 4.0$	$56.6 \pm 4.6$	$74.9 \pm 4.0$	$7.7 \pm 1.2$	$1.7 \pm 0.2$
7–12 days	$46.7 \pm 3.5$	$62.5 \pm 3.5^a$	$86.1 \pm 2.0$	$8.6 \pm 0.9^a$	$1.7 \pm 0.2^a$
Available	$46.0 \pm 3.4$	$55.7 \pm 3.9$	$80.6 \pm 3.3$	$10.7 \pm 1.6$	$1.7 \pm 0.2$
13–20 days	$49.9 \pm 2.6$	$73.0 \pm 2.7^{ab}$	$84.8 \pm 2.9$	$13.7 \pm 1.8^a$	$1.6 \pm 0.2^a$
Available	$52.9 \pm 3.3$	$66.1 \pm 3.3$	$84.1 \pm 2.8$	$14.7 \pm 1.9$	$1.9 \pm 0.2$
21–36 days	$56.9 \pm 2.7$	$78.8 \pm 2.5^a$	$78.5 \pm 3.7^b$	$15.3 \pm 1.4^a$	$1.1 \pm 0.2^{ab}$
Available	$53.5 \pm 3.3$	$77.4 \pm 2.2$	$88.5 \pm 2.5$	$16.2 \pm 1.4$	$2.0 \pm 0.2$
0–36 days	$51.0 \pm 1.4$	$68.1 \pm 1.6^{ab}$	$82.0 \pm 1.5$	$12.0 \pm 0.7^a$	$1.6 \pm 0.1^{ab}$
Available	$50.9 \pm 1.6$	$63.3 \pm 1.7$	$83.3 \pm 1.4$	$12.5 \pm 0.7$	$1.9 \pm 0.1$

<sup>a</sup> 85% CI of variable did not overlap zero in univariate, generalized linear mixed models with use (fledgling locations vs. nest) as the response variable.

<sup>b</sup> Included in top habitat selection (fledgling locations vs. *available*) model and 85% CI did not overlap zero.



**TABLE 2.** Best-supported habitat selection models for each of the 6 fledgling age classes and includes Akaike's information criterion values (adjusted for small sample size;  $AIC_c$ ) along with  $\beta$  slopes and 85% CI values for all important habitat variables (85% CI of  $\beta$  slope not overlapping zero). Mid = mid-story cover, Over = overstory cover, BA = stand basal area, Water = distance to water body, Sap = sapling cover, Aspect = Beers' slope aspect, Gap = distance to canopy gap, Max. DBH = maximum diameter at breast height.

Model	$\Delta AIC_c$	$K$	$w_i$	Variable	$\beta$	85% CI
<b>Ages 0–36 days</b>						
Mid + BA + Water	0.00	6	0.97	Mid	0.007	0.003 to 0.012
Null	35.07	3	0.03	BA	−0.016	−0.027 to −0.005
				Water	−0.115	−0.202 to −0.028
<b>Ages 0–2 days</b>						
CH + Sap	0.21	5	0.97	CH	−0.123	−0.204 to −0.042
Null	6.82	3	0.03	Sap	0.028	0.014 to 0.042
<b>Ages 3–6 days</b>						
Aspect + Sap	0.00	5	0.21	Aspect	0.637	0.048 to 1.225
Sap	0.29	4	0.18	Sap	−0.016	−0.026 to −0.005
BA <sup>2</sup> + BA + Aspect	0.43	6	0.17	BA <sup>2</sup>	−0.202	−0.386 to −0.017
BA + Aspect	1.25	5	0.11	BA	0.393	0.083 to 0.703
BA <sup>2</sup> + BA	1.41	5	0.10	Gap	0.055	0.010 to 0.099
Aspect + Gap	1.46	5	0.10			
Gap	1.84	4	0.08			
Null	2.76	3	0.05			
<b>Ages 7–12 days</b>						
Max. DBH + Aspect	0.00	5	1.00	Max. DBH	0.047	0.021 to 0.072
Null	12.10	3	0.00	Aspect	0.749	0.301 to 1.198
<b>Ages 13–20 days</b>						
CH + Sap + Mid	0.00	6	0.66	CH	−0.069	−0.115 to −0.023
CH + Sap	1.59	5	0.30	Sap	−0.015	−0.024 to −0.006
Null	5.40	3	0.04	Mid	0.014	0.003 to 0.025
<b>Ages 21–36 days</b>						
BA <sup>2</sup> + BA + Water + Aspect	0.00	7	0.34	BA <sup>2</sup>	0.003	0.001 to 0.004
BA <sup>2</sup> + Water	0.02	6	0.34	Water	−2.662	−3.765 to −1.560
Water + BA + Aspect	1.09	6	0.20	Aspect	0.692	0.152 to 1.232
Water + Sap + Over	1.99	6	0.13	BA	−0.050	−0.080 to −0.020
Null	40.28	3	0.00	Sap	0.021	0.007 to 0.034
				Over	−0.021	−0.035 to −0.007

locations. Differences between habitat measurements associated with nests vs. fledgling locations were less common in the 0–2 days age class (2 differences) compared with older age classes (4–5 differences; see Table 1).

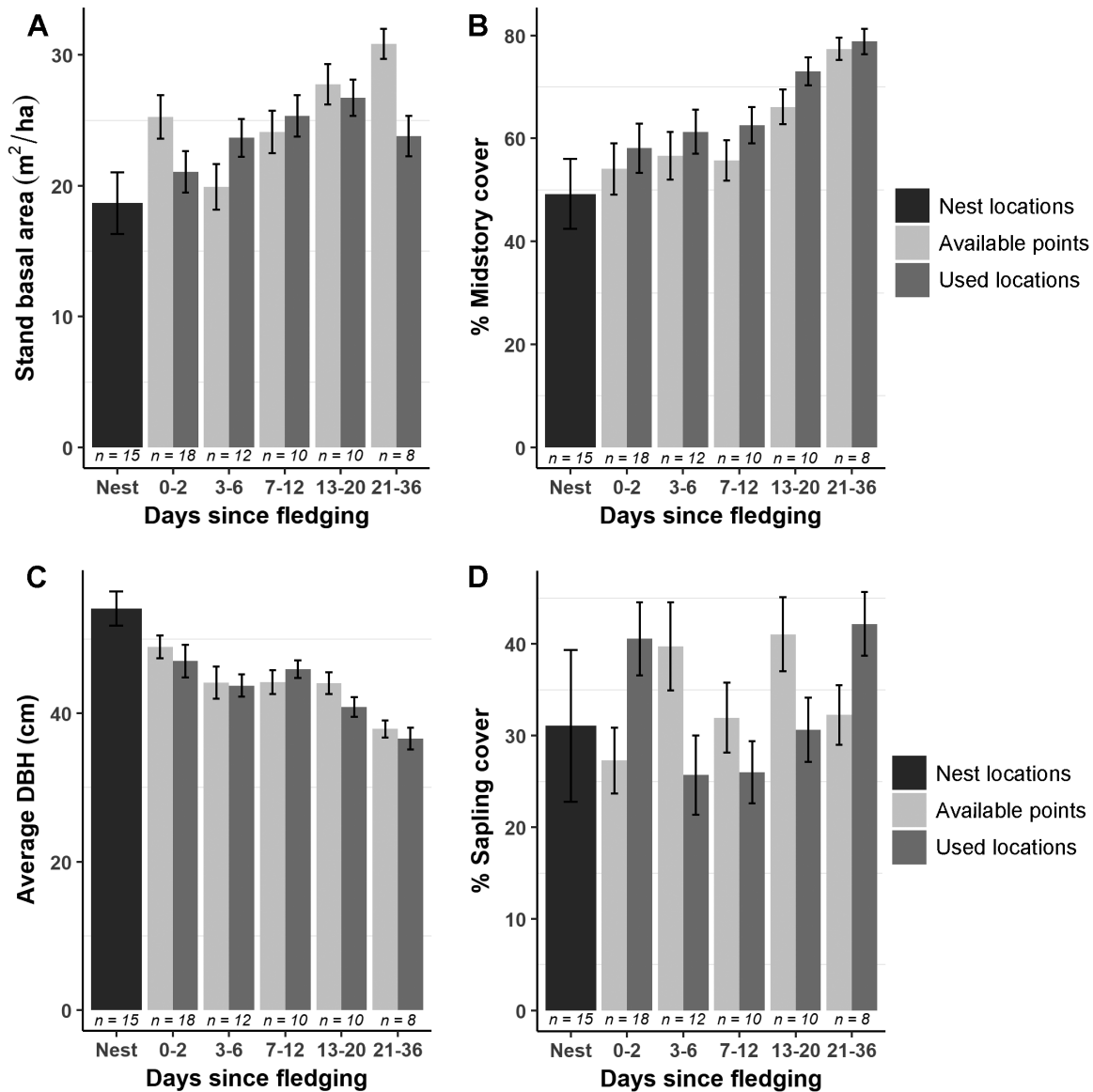
### Post-fledging Survival

Of the 20 fledglings tracked, we documented mortality for 10 birds. We attributed at least 9 mortalities to predators: eastern chipmunks (*Tamias striatus*) were the most common (7 deaths, all during 0–4 days post-fledging); one fledgling was killed by a Sharp-shinned Hawk (*Accipiter striatus*; 16–17 days; transmitter recovered under the hawk's nest), and another by an unknown predator (7–8 days). Evidence for chipmunk depredation involved following transmitter signals to active chipmunk burrows or finding transmitters/harnesses or partially eaten fledglings near burrows. We were unable to attribute one mortality to any cause: on the day after fledging, the bird was discovered in the Allegheny River 60 m from the location at which it was captured. Finally, we were unable to relocate one fledgling after 16 days post-fledging, so its fate was unknown.

Survival from 0–2 days post-fledging was lower than survival from 3–17 days, regardless of sample size (14 independent or 20 total fledglings), with one top competing model from the reduced dataset further differentiating between survival of ages 3–6 days and 7–17 days; Appendix Table 3). Of the 2 top models from the reduced dataset, daily survival varied between ages 0–2 days (0.79, 85% CI: 0.66 to 0.90) and either ages 3–17 days (0.98, 85% CI: 0.96 to 1.00) or ages 7–17 days (0.99, 85% CI: 0.97 to 1.00). Cumulative survival of the 17-day period was  $0.48 \pm 0.14$  when considering only the 14 independent fledglings and  $0.49 \pm 0.11$  when considering all 20 fledglings.

Over the initial 3 days of highest mortality, sapling cover, canopy height, and BA were each included at least once in the top 3 equivalent models of habitat variable influences on survival (with canopy height included in all 3; Appendix Table 3A). However, only the 85% CI for canopy height (−0.95 to −0.16) did not overlap zero. Canopy height in areas used by the 5 fledglings from unique broods that died during this period was  $33.9 \pm 1.0$  m, compared with  $28.3 \pm 0.9$  m used by the 9 survivors. For the full sample of 20 fledglings (including siblings), there were 2 top





**FIGURE 2.** Dynamic habitat selection for 4 habitat variables (mean  $\pm$  SE) across 5 age classes (days since fledging) of Cerulean Warbler fledglings radio-tracked in northwestern Pennsylvania, USA. **(A)** Fledglings used areas with greater basal area (BA) than nesting habitat, especially at older ages, but selected for lesser BA compared with available habitat at 0–2 days and 21–36 days post-fledging. **(B)** Fledglings used areas with greater mid-story cover compared with both nest habitat and available habitat and **(C)** used smaller average DBH (diameter at breast height) trees compared with nesting habitat but did not show strong selection compared with available habitat. **(D)** Fledglings selected for areas with greater sapling cover at 0–2 days and again at 21–36 days, but for areas with lesser sapling cover from 3 to 20 days.

equivalent models (Appendix Table 3A), and once again there was a negative relationship between canopy height and survival (85% CI:  $-0.70$  to  $-0.16$ ).

### Nest Survival and Productivity

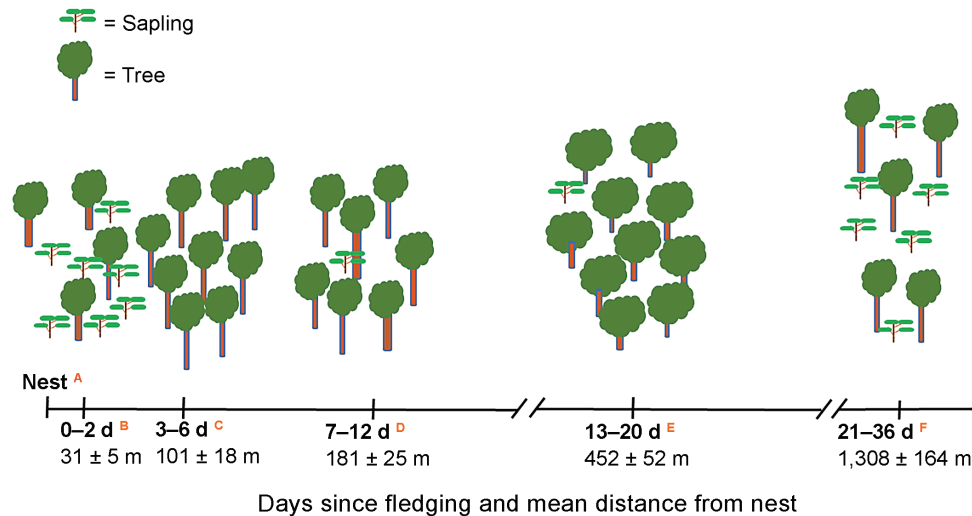
Daily nest survival in 2014 (0.952,  $n = 35$ , 85% CI: 0.938 to 0.965) was similar to nest survival in 2015 (0.966,  $n = 29$ , 85% CI: 0.953 to 0.978), and the daily nest survival for the 2 years combined was  $0.958 \pm 0.007$ . Cumulative nest

success was  $34.5 \pm 4.4\%$ . Number of fledglings produced per successful nest was  $2.96 \pm 0.15$ .

### DISCUSSION

#### Fledgling Movement

Cerulean Warbler fledglings increased their daily movements as they aged, as expected and similar to other forest warbler species (e.g., Vitz and Rodewald 2010). However,



**FIGURE 3.** Dynamic habitat selection behavior by Cerulean Warbler fledglings across a heterogeneous forest landscape. Areas with greater sapling cover are represented by more sapling figures in an area. Areas with greater BA (basal area) and fewer canopy gaps are represented by more (and closer together) trees. Relative DBH (diameter at breast height) and tree height of trees in the preferred areas are indicated by trunk width and height. Greater mid-story cover is indicated by larger crowns. Potential forest management practices resulting in vegetation patterns used by each age class: A = shelterwood harvests, group selection, or stand thinning within even-aged forests (promotion of uneven canopy); B = promotion of sapling regeneration through similar methods as A; C = limiting size or adapting shape of harvests to allow young fledglings to access closed canopy stands with dense midstory; D = retention of some large-diameter trees; E = retention of stands with dense midstory; F = maintaining of stands with intermediate BA (e.g.,  $23.8 \pm 1.6 \text{ m}^2 \text{ ha}^{-1}$  used by fledglings) and maintaining forested riparian habitat.

both maximum and mean dispersal distances from nests for the Cerulean Warbler fledglings (mean =  $2.4 \pm 0.7$  km, maximum = 5.3 km through  $28.1 \pm 1.8$  days, maximum = 36 days) were considerably greater than what was reported for Ovenbirds (mean = 1.3 km, maximum = 3.7 km through 29 days), Worm-eating Warblers (*Helminthos vermivorum*; mean = 1.1 km, maximum = 1.8 km through 29 days; Vitz and Rodewald 2010), and Golden-winged Warblers (*Vermivora chrysoptera*; means =  $1.0 \pm 0.4$  km and  $0.9 \pm 0.1$  km; through a maximum of 35 days, at 2 study areas; Fiss 2018). Interestingly, the Cerulean Warbler fledgling that moved the greatest distance from its nest site (5.3 km at 27 days post-fledging) returned to its natal area (where it had previously been accompanied by a parent) at 28 days post-fledging. This individual then remained closer (158–652 m) to its nest, seemingly independent at this point and foraging in mixed-species flocks, until 37 days when its transmitter's battery life expired.

### Habitat Selection

**Dynamic post-fledgling habitat selection.** The age-specific patterns of habitat selection we observed throughout the post-fledging period exemplify the importance of creating and maintaining structurally diverse forests on the breeding grounds. It is unclear how much of the following habitat selection behavior reflects fledgling vs. parental decisions while fledglings were located with

one or both parents (but see Vega Rivera et al. 2000 and McNeil et al. 2019). Thus, we refer to selection by family groups that include parent(s) and fledgling(s). During 0–2 days post-fledging, family groups selected for areas with greater sapling cover and shorter canopy height compared to available areas, with some (<50% of observations) individuals observed in the understory. At this age, young fledglings are not very mobile and are thus limited to an area within a short distance from their respective nests. The selection for greater sapling cover is similar to adult territory and nest-site selection reported from previous studies; adult Cerulean Warblers selected for territories and nest sites with greater understory density (Hartman et al. 2009, Boves et al. 2013a), possibly to provide protection for fledglings. By days 3–6, family groups demonstrated increased mobility and were able to select habitat farther from the nest. Family groups during this time interval preferred areas with less sapling cover and greater basal area compared to randomly available habitat, which reflects stands of closed-canopy mature forest. From days 7–12, sapling cover and basal area did not differ between used and available locations, but fledglings used areas with larger trees and were usually found in the mid-story to overstory. From days 13–20, selection occurred for areas with greater mid-story cover, lower average canopy height, and less sapling cover compared with randomly available habitat (Figure 3). This behavior was in opposition to both adult breeding territory selection and selection patterns

the same fledglings exhibited at younger ages, and these favored structural characteristics are often associated with even-aged stands of mid-successional (e.g., ~20–40 yr old) forest in this region.

From day 21 until the end of the tracking period, fledglings made the transition to independence. The 8 fledglings we tracked within this age class were usually found in mixed-species flocks, with or without their parent, and most had moved downslope to areas closer to permanent water sources (specifically the Allegheny River, Kinzua Reservoir, or Tionesta Creek), perhaps reflecting greater invertebrate prey availability in these riparian areas (Burdon and Harding 2008, Mitchell et al. 2010, Dittmar et al. 2014) and more cover from predators (i.e. increased leaf biomass, Bolstad et al. 2001). The fledglings no longer selected for increased mid-story cover but did select for decreased basal area and increased sapling cover, indicating that perhaps the fledglings were making the transition into adult habitat selection behavior and potentially could have been prospecting for future breeding sites (Reed et al. 1999).

**Post-fledgling vs. nesting habitat selection.** Cerulean Warbler fledglings we monitored used some stands with structure similar with areas used for nesting, especially in mature, unharvested forest stands on the steep river valley slope. In these areas, natural heterogeneous canopy structure caused by treefalls (de Lima and de Moura 2008) often exists, but with greater mid-story cover than is provided by many managed stands used for nesting (e.g., first stage shelterwood harvests, Newell and Rodewald 2012). However, we also observed fledglings using some stands that differed structurally from what is commonly used by nesting Cerulean Warblers (e.g., ~25-yr regenerating forest; Wood et al. 2005; Figure 3 and Table 1), with smaller and more numerous trees, fewer canopy gaps, and greater mid-story cover. Use of areas with more trees and greater mid-story cover than adult territories could be related to both increased food availability and increased protection from predators (Vitz and Rodewald 2007, McDermott and Wood 2010).

### Post-fledging Survival

Our estimate of  $48 \pm 14\%$  survival of the first 17 days post-fledging is at the midpoint of the range reported in a review of post-fledging passerine survival (Cox et al. 2014). Most (7/10) of our documented depredations were of fledglings that were last seen on or near the ground. We did, however, also observe one instance of a non-radio-tagged fledgling depredated in the overstory canopy by a Red-bellied Woodpecker (*Melanerpes carolinus*) shortly after the fledgling left its nest. Survival of fledglings after 17 days post-fledging likely fell between our  $98.2 \pm 1.3\%$  ( $n = 14$ ) daily survival estimate (~88% weekly survival) from 3 to 17 days post-fledging and our weekly apparent survival

estimate for adult males at the same study site over the same time period ( $96.8 \pm 2.6\%$ ,  $n = 53$ ; Raybuck et al. 2017).

We found a negative relationship between canopy height and fledgling survival over the initial 3 days post-fledging. The mechanism behind this relationship is unclear, but no matter the mechanism, it may explain why fledglings selected for lower average canopy height during 0–2 days post-fledging. Due to our low sample size, we may have lacked the statistical power to detect other important relationships between habitat structure and survival, and thus further investigation is warranted. For example, sapling cover (included in one top competing model, see Appendix Table 3) had little explanatory power (85% CI of  $\beta = -0.02$  to 0.05). However, 3 of 7 fledglings that were depredated over this period were last seen on or near the ground in areas with 0–10% sapling cover, which potentially exposed the fledglings to understory-dwelling predators. Meanwhile, all 13 fledglings that survived this period were associated with areas with >10% (mean  $35.7 \pm 5.2\%$ ) sapling cover, which supports the suggestion that stands providing understory cover offer protection from predators for young fledglings that descend from the canopy (Nicholson 2003, Wood et al. 2013). The eastern chipmunk, a primarily ground-dwelling species, was identified as the most common predator of fledglings in our study, although it is possible that other predators are more common in other breeding regions. Chipmunks were so numerous in our study years that they were detected during nest checks in nearly all adult territories. Chipmunks have also been identified as predators of fledglings of other forest-dwelling passerines (e.g., King et al. 2006, Moore et al. 2010, Vitz and Rodewald 2011), and their predation pressure on avian nest and fledgling survival varies dramatically with interannual variation in chipmunk abundance, which closely tracks yearly acorn mast levels and has the potential to affect avian abundance (Schmidt and Ostfeld 2003).

Our post-fledging survival estimate ( $48 \pm 14\%$ ) should be used with some caution. First, this estimate is derived from a relatively small sample size and just 2 years. Post-fledging survival may fluctuate dramatically among years (Schmidt and Ostfeld 2003) or between regions (Fiss 2018) and thus its relative contribution to population dynamics may vary substantially as well. As previously stated, we were unable to capture many of the most mobile fledglings that did not come down from the canopy upon fledging. Thus, future full-life-cycle modeling and sensitivity analyses should treat our estimate as a probable minimum estimate of post-fledging survival.

### Conservation and Management Implications

We documented dynamic habitat selection patterns during the post-fledging period and structural differences between nesting and post-fledging habitat. Forest management practices that promote a heterogeneous forest

structure composed of stands in various stages of regeneration and structural conditions will enable the dynamic nature of Cerulean Warbler post-fledging habitat selection behavior. When utilizing shelterwood harvests or forest stand improvements to create Cerulean Warbler nesting habitat within landscapes dominated by even-aged, closed-canopy forest conditions that are common throughout much of the Appalachian breeding region (e.g., creating habitat with 9–21 m<sup>2</sup> ha<sup>-1</sup> residual basal area; Wood et al. 2013), efforts should be made to ensure that fledglings have access to sapling regeneration within the managed stand as well as access to adjacent stands with greater mid-story cover. In many instances, this scenario of dense mid-story cover and high BA adjacent to partial timber harvests will already be present or has potential to be created, as the purpose of partial timber harvests (e.g., shelterwood harvests) is to promote understory regeneration through gradual reduction of canopy tree basal area and removing competing mid-story vegetation to increase sunlight levels (Nyland et al. 2016). Nonetheless, it is important to realize that fledgling survival may be lower in the initial years following a first-stage shelterwood harvest compared with subsequent years after regeneration has progressed in height and density. Furthermore, in large first-stage shelterwood harvests (e.g., >75 ha), fledglings that leave nests located in the interior portion of the harvest have farther to travel before reaching preferred areas with dense mid-story cover, fewer canopy gaps, and higher basal area (beginning at 3–6 days post-fledging), highlighting the importance of careful planning of diverse forest composition and structure. For instance, decreasing the distance from the center of a large shelterwood harvest to intact mature forest (i.e. limiting its size or modifying its shape) may benefit fledglings, but we encourage further investigation of this hypothesis. Finally, because we documented 1.0–5.3 km (mean 2.4 ± 0.7 km) post-fledging dispersal distances, and because Cerulean Warbler adults have been known to favor large tracts of forest for nesting (Wood et al. 2013), ensuring that extensive forested tracts are available in landscapes where Cerulean Warbler conservation is a management objective should benefit this species.

We believe the general recommendations listed above can improve guidance to land managers who desire to provide habitat for Cerulean Warblers that meet the needs across the full reproductive cycle. These recommendations should not only improve Cerulean Warbler habitat management efforts, but they also agree with current management strategies for several other avian species that use a heterogeneous mixture of forest conditions throughout the nesting and post-fledging seasons (Anders et al. 1998, Wilson and Watts 2008, Chandler et al. 2012), including other species of concern (e.g., Wood Thrush and Golden-winged Warblers).

Furthermore, these recommendations align with the much broader conservation goal of protection of overall forest biodiversity through stand age class diversification and increased structural complexity (Lindenmayer et al. 2000, Shifley et al. 2014).

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**Ethics statement:** We captured, handled, and marked all birds under all necessary federal (USGS banding permit #s 23877 and 23277) and state permits, following Arkansas State University Institutional Animal Care and Use Committee Protocol No. 574486-1.

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**Data depositary:** Analyses reported in this article can be reproduced using the data provided by Raybuck et al. (2020).

**Conflict of interest statement:** The authors declare that there are no conflicts of interest regarding this study or manuscript.

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**APPENDIX TABLE 3.** Best-supported known-fate survival models summarize the top equivalent survival models for (A) effects of top habitat covariates from the habitat selection analysis on survival during ages 0–2 days post-fledging, and (B) variation in survival rate by age class compared over ages 0–17 days post-fledging. Models ranked by Akaike’s information criterion (adjusted for small sample size; AICc).  $w_i$  = model weight,  $k$  = number of parameters, CH = canopy height, Mid = Mid-story cover, BA = stand basal area, Sap = sapling cover.

A. Habitat covariate effect							
Ages 0–2 days ( $n = 20$ )				Ages 0–2 days ( $n = 14$ )			
Model	$\Delta AIC_c$	$w_i$	$k$	Model	$\Delta AIC_c$	$w_i$	$k$
CH	0.00	0.72	2	CH	0.00	0.50	2
CH + Mid	1.93	0.27	3	CH + BA	1.10	0.29	3
Constant	8.91	0.01	1	CH + Sap	1.89	0.20	3
				Constant	7.70	0.01	1
B. Age class effect							
Ages 0–17 days ( $n = 20$ )				Ages 0–17 days ( $n = 14$ )			
Model	$\Delta AIC_c$	$w_i$	$k$	Model	$\Delta AIC_c$	$w_i$	$k$
d0–2, d3–17	0.00	1.00	2	d0–2, d3–17	0.00	0.70	2
Constant	13.09	0.00	1	d0–2, d3–6, d7–17	1.76	0.29	3
				Constant	9.35	0.01	1